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Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation

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Abstract

Fragmentation in seagrass systems results in changes to landscape features that may have implications for fauna. We examine published studies to identify whether faunal abundance shows any relationship with patch size of seagrass beds, suggesting preferential use of the edge or interior by seagrass associated taxa. In a series of studies in Tampa Bay, FL, we also examined: (1) the relationship between abundance of both fish and amphipod fauna and seagrass patch size in 24 seagrass (Halodule wrightii) beds (5-93 m²) in 1994 and 1995; (2) whether abundance of the infaunal polychaete, Kinbergonuphis simoni, was significantly different within the 1 m edge versus interior of two seagrass (Halodule wrightii) beds of similar size and age; and (3) compared the spatial distribution of the tube-building polychaete, Spirorbis spirillum, in Thalassia testudinum seagrass beds in two sites in Tampa Bay. Neither review of the published literature on fauna and seagrass patch size nor the data presented from our Tampa Bay studies suggest that habitat fragmentation has any consistent impact on fauna over the spatial scales that have been investigated. Likewise, little evidence exists that identifies any taxonomic group to be fragmentation sensitive in that they differentially utilized edge or core areas of seagrass patches. While we did detect a reduction of both infaunal and epibenthic polychaetes at the 1 m edges of seagrass beds relative to interior areas, the reduction was not similar along all edges. Events such as seagrass die off or a high incidence of boat propeller-damage over an extensive area may be required to detect effects of habitat fragmentation on fauna. Given that patch size alone does not appear to adequately account for variation in faunal abundance, we suggest that restoration efforts might best focus upon locating areas with similarity of landscape context or patch characteristics other than patch size. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Faunal response; Fragmentation; Seagrass; Conservation

1. Introduction

Fragmentation, which results in both habitat loss and a change in habitat configuration (Villard et al., 1999), is an important factor thought to contribute to the loss of biodiversity (Wilcox and Murphy, 1985). Fragmentation of vegetated habitats which results in an increase in the number of patches but also a decrease in mean patch size (Trzcinski et al., 1999) has been linked to changes in faunal spatial distribution or patterns of species abundance in many systems (Robinson et al., 1992; Herkert, 1994; Vos and Stumpel, 1995). As habitats fragment the proportion of edge to interior in any given

patch should also increase (e.g. Forman, 1995; Trzcinski et al., 1999). Thus, as these habitat changes occur, a variety of responses by fauna may be expected depending on whether species have fidelity to the interior sections of habitat or if they preferentially utilize the ecotone along patch edges (Bender et al., 1998). Identification of species that prefer edges versus the interior of a habitat may be inferred from observation or sampling of fauna at these spatially distinct locations within patches. Alternatively, studies that include information on faunal abundance in different patch sizes, may record more individuals per unit area as patch size decreases. Of interest are disproportionate increases in faunal density related to changes in the ratio of edge to interior regions of patches.

Edges as areas of enhanced species interactions (i.e. pollination, predation, competition) have emerged as an important topic in conservation ecology (e.g. Saunders et

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al., 1991; Fagan et al., 1999), given that anthropogenic impacts often result in fragmented habitats. Knowledge of spatially skewed responses to habitat "cores" or edges by fauna, including modification of species dispersal by habitat edges, may be of critical importance in a number of conservation issues especially when accurate prediction of the impacts of alteration of landscape patch size are of interest (Mazarolle and Villard, 1999). Understanding the role of edges may also be important in restoration efforts if constructed habitats differ in size and shape from natural areas (Bell et al., 1997). Specifically, evaluating the success of restoration efforts when patch sizes of restored and reference areas differ may be problematic if target species display preferences for edge or interior regions of a habitat.

Habitat fragmentation, especially as a result of habitat loss from human activities, has been addressed across a broad expanse of terrestrial habitats, but comparatively less information is available from marine settings (Frost et al., 1999). This may be related to the fact that humans are thought to impact both autotrophs and herbivores in terrestrial systems whereas human impacts in marine systems have largely been focused on removal of high trophic levels (overfishing, etc.; Allison et al., 1998). However, there is considerable information on changes in distributions of subtidal vegetation, such as seagrasses (e.g. Pulich and White, 1991), which have received recent attention because of the role of seagrasses in supporting coastal ecosystems (Thayer et al., 1984) and increasing threats from anthropogenic activities (Short and Willy-Echerverria, 1996). Fragmentation of seagrasses has been reported as a result of disease (Wilson, 1949) and human recreational activities (e.g. Hastings et al., 1995) and thus abundance of fauna associated with seagrass beds might exhibit different patterns depending on their behavior and use of habitat edges, as has been shown for selected taxa in other habitats.

Herein we review the literature that focuses on patch size in seagrass systems and associated fauna to evaluate whether faunal abundance shows any relationships with patch size, suggesting preferential use of the edge or interior by seagrass associated taxa. Next, we summarize our investigations in Tampa Bay, FL, that expand upon the studies on faunal-seagrass patch size relationships and edge/interior preference by fauna. Finally, we compare our results with those from terrestrial habitats and discuss our findings with respect to planning and evaluating seagrass conservation and restoration in general.

2. Materials and methods

2.1. Literature survey

We used key word (seagrass, patch, fragmentation) searches to identify journal articles and doctoral dis-

sertations that addressed issues of fragmentation or patch size and fauna in seagrass habitats. We reviewed the results of the studies and tabulated information on the type of fauna and whether the work was conducted in natural seagrass beds or with patches composed of artificial seagrass structure. Finally, we categorized the results of the studies with respect to any "preference" shown by fauna for edges or interior of seagrass beds. Preference for a location within a bed was defined as an increase in faunal abundance or growth, or improved survival from predation (refuge) as determined from survey or experimental studies.

2.2. Tampa Bay studies

2.2.1. Epibenthic fauna and patch size survey

A survey of faunal use of natural seagrass patches was performed in the spring and fall of 1994 and 1995. The study site was a 100×400 m area located within the seagrass landscape in Tampa Bay, Florida (27°45′N, 83°38′W). Detailed maps of the study area are available in Robbins and Bell (2000). Twenty-four discrete beds of Halodule wrightii ranging in size from 5–93 m² were sampled on each of the four sampling dates to determine fish and epibenthic amphipod abundance. Fish abundance was determined with the use of a 1×1 m drop trap consisting of 2-mm mesh sides (sensu Fonseca et al., 1996). Three drop trap samples were haphazardly deployed within each bed, except in the smallest bed where only one trap could be deployed because of logistical limitations. A dip net (2 mm mesh) was used to sample all fish within the trap. All fish were enumerated and identified to species. Amphipod abundance (No./m²) was determined with the use of a modified epibenthic sampler (Virnstein and Howard, 1987; opening 0.5×0.25 m) that collected both blades and associated fauna above the sediments. Three samples were haphazardly taken outside of droptraps within each bed and all amphipods were enumerated and identified to species with the aid of a dissecting microscope.

Linear regressions of total fish abundance/m² versus patch size were conducted for the fall and spring seasons separately and then all dates combined. A similar approach was used to examine patch size versus abundance of the most dominant (composing >85% of all individuals) species. Data were transformed if necessary to meet assumptions of normality and homogeneity of variances. Slopes of simple linear regressions were examined to determine whether patches with proportionately more edge (e.g. small patches) or interior (e.g. large patches) resulted in enhanced densities of organisms. This same approach was used to evaluate relationships between abundance of total amphipods and dominant species of amphipods with patch size.

2.2.2. Edge/interior patterns of abundance for infaunal and epifaunal polychaetes

Habitat use of the infaunal polychaete, Kinbergonuphis simoni, was determined by examining abundances within the 1 m edge versus interior (9 m from the edge) of two seagrass (*Halodule wrightii*) beds approximately 20×20 m located within a 100 m×100 m area in Lassing Park, FL, within Tampa Bay, FL (27°47′N, 82°37′W). This polychaete is a small tube builder which broods its young and is found almost exclusively in seagrass beds (Bell et al., 1993). In June 1990, 12 sediment cores (7.5 cm diameter, 15 cm deep) were taken within the edge and interior of each bed. Sediment cores were washed over a 0.5-mm sieve in the field and all individuals of *Kinbergo*nuphis simoni were enumerated in the laboratory under a dissecting microscope. Abundances of K. simoni were compared at the edge and interior of each bed using a t-test. There were no other beds of identical dimension or age within this location and our inference in this case is limited to beds of this size and age at Lassing Park.

Habitat use of the epibenthic polychaete, Spirorbis spirillum, was determined within two natural Thalassia testudinum seagrass beds located at Bunces Pass (27°39′N, 82°43′W) and Shore Acres (27°49′N, 82°36′W), Florida. Spirorbis spirillum is a tube-building epibiont attached to seagrass blades and this taxon broods it larvae until released to the plankton for a very short duration (min; Dirnberger, 1990). Ten seagrass blades were collected at 1 m intervals along a transect spanning the longest axis of each seagrass bed. Mean density of S. spirillum per blade of seagrass was determined for each meter along the transect. Density of S. spirillum was compared with a nonparametric one-way analysis of variance (Kruskal-Wallis test) to determine if it differed significantly among locations along each transect. If significant differences were detected by the Kruskal-Wallis test, then a Dunn's multiple comparison test (a Bonferroni technique which has a conservative experiment wise error rate) was used to determine which densities were different among locations along each transect.

3. Results

3.1. Literature review

A number of landscape ecology studies in subtidal seagrass beds using both natural settings and experimental approaches provide information about fauna/patch size relationships (Table 1). Only one study has directly assessed faunal response to a fragmenting habitat (Robbins, 1998a) in which hermit crabs were not found consistently to alter their abundance per unit area when 40% of the habitat was removed and more edges created. Other studies have indirectly assessed the impact of fragmentation on a variety of fauna through sampling studies of seagrass patches or experimental manipula-

tions. As outlined in Table 1, experiments on colonization of seagrasses patches of different sizes have indicated that some faunal taxa may be edge-loving while others show preference for interior sectors of patches, or no preference at all. In a survey of fish and macroinvertebrate abundance versus patch size, McNeill and Fairweather (1993) reported that some species of fish and macroinvertebrates were disproportionately abundant in small versus large patches. Hovel's (1999) experiments illustrated that juvenile blue crab survival was highest in smallest patches of seagrass although this stands in contrast to Eggleston et al.'s (1998) studies on blue crabs and patch size. Other studies have performed sampling within patches to assess whether species distributions were spatially anisotropic with increased abundances at edges or center of seagrass beds (e.g. Bologna and Heck, 1999) but with some mixed results. Finally, experimental studies on growth/survival of faunal taxa at seagrass bed edges found increased survival and growth for one of the taxa (Irlandi, 1994) or an increased growth but higher risk of predation in the other (Bologna and Heck, 1999).

3.2. Tampa Bay studies

3.2.1. Epibenthic fauna and patch size survey

The density of fish across seagrass beds of varying size displayed marked seasonal differences (Fig. 1). Density of fish was relatively consistent across all patch sizes in fall samplings and showed little change as patch size increased. In spring samplings total fish (all species) density was generally higher than that observed in the fall with highest densities recorded in beds of 80 m² (Fig. 1). Much of the density patterns observed for total fish was reflected in patterns of abundance by *Gobiosoma robustum* (Fig. 1). Regression analysis showed no significant relationship of total fish or goby density and patch size (Table 2).

Total amphipod density displayed a significant positive relationship with seagrass bed size in the fall (Fig. 2, Table 2) but not in the spring (Table 2). Among the three species of amphipods which were most abundant in spring and fall samplings, both *Cymadusa compta* and *Cerapus tubularis* generally displayed higher densities in the spring than fall regardless of patch size, while seasonal differences were not consistent for *Ampithoe longimana*. No significant relationship between seagrass bed size and density of any amphipod species was recorded in either spring or fall (Table 2, Fig. 2). The r^2 values were extremely low and highest amphipod density for all three species in the spring were in beds of intermediate size (30–70 m²).

3.2.2. Edge/interior patterns of abundance for infaunal and epifaunal polychaetes

Density of the infaunal polychaete, *Kingbergonuphis simoni*, in sediment core samples ranged from 1 to 52

Table 1
Results from previous studies that examine faunal-patch size relationships in seagrass beds^a

Taxa examined	Author	Natural or artificial seagrass units (ASU)	Preference
Bivalves			
Hard clams	Irlandi (1996)	Natural	Interior
Hard clams	Irlandi (1997)	Natural	Interior
Hard clams	Irandi (1997)	ASU	Neither
Bay scallop	Irlandi et al. (1995)	Natural	Neither
Bay scallop	Irlandi et al. (1999)	Natural	Neither
Bay scallop	Bologna and Heck (1999)	Natural	Edge
Crustaceans			
Hermit crabs	Robbins, (1998a)	ASU	Neither
Juvenile blue crabs	Eggleston et al. (1998)	ASU	Interior
Juvenile blue crabs	Hovel (1999)	ASU	Edge
Penaeid shrimp	Eggleston et al. (1998, 1999)	ASU	Edge
Amphipods/isopods	Eggleston et al. (1999)	ASU	Edge
Macroinfauna			
Multiple species	Frost et al. (1999)	Natural	Neither
Fish			
Multiple species	Eggleston et al. (1999)	ASU	Neither
Multiple species	McNeill and Fairweather (1993)	ASU	Edge

^a Edge or interior refers to preference by fauna based either on density, growth or refuge from predation; neither indicates no preference at edge or interior.

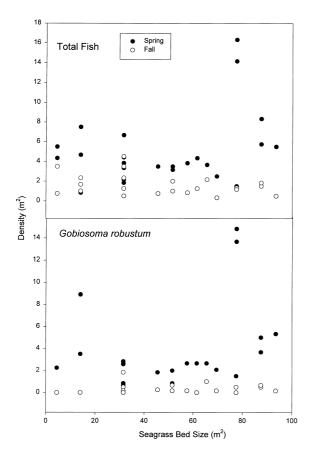


Fig. 1. Seasonal densities for total fish and *Gobiosoma robustum* within *Halodule wrightii* beds of various sizes, spring and fall 1994–1995.

individuals. In both seagrass beds at Lassing Park, mean density of K. simoni was highest in cores taken from the center of beds compared to those taken from edges (Fig. 3). In bed 1 densities in the center of the bed were significantly greater than at edges (approximately 4 times higher; t-test, 22 d.f., P=0.005). In bed 2 mean densities in the center of the bed were also significantly greater than at the edges (t-test, 22 d.f., t<0.001). Note that mean densities of t<6 dispersion t dispersion t<6 dispersion t<6 dispersion t<6 dispersion t<6 dispersion t<6 dispersion t

Density of the epibenthic polychaete *Spirorbis spirillum* indicated a lower abundance at one edge (L) of the bed at Bunce's Pass (Fig. 4). Specifically, densities of *S. spirillum* were very low within the first 1 m of the seagrass bed. The Kruskal–Wallis test indicated a significant difference among locations along the transect. The Dunn's multiple comparison test showed that densities at L1 were significantly lower than densities at L2, L3, L7 and L10 (Dunn's test, P < 0.05). Samples from R1 were not significantly different from any other R location. However densities of *S. spirillum* from R6 were significantly different from R3, R 13, and R 14. No significant differences in the density of *S. spirillum* were detected along the transect at Shore Acres (Kruskal–Wallis, P > 0.05; Fig. 4).

4. Discussion

Neither review of the published literature on fauna and seagrass patch size nor the data from our Tampa

Table 2 Summary of regression analysis for fish and amphipod fauna versus seagrass patch size in fall and spring 1994 and 1995

TAXA	Slope	r^2 Value	P value
Total fish			
Fall	1.886	0.108	0.177
Spring	-0.15	0.05	0.264
Gobiosoma robustum			
Fall	0.041	0.049	0.295
Spring	0.063	0.143	0.068
Total amphipods			
Fall	1934.0	.242	0.017
Spring	0.014	0.010	0.647
Ampithoe longimana			
Fall	0.533	0.111	0.112
Spring	0.020	0.010	0.647
Cymadusa compta			
Fall	0.048	0.02	0.434
Spring	0.002	0.001	0.938
Cerapus tubularis			
Fall	0.171	0.06	0.242
Spring	-109.6	0.004	0.764

Bay studies suggest that patch size has any consistent impact on resident fauna over the spatial scales that have been investigated (e.g. <1 m² to >5000 m²). Likewise, little evidence exists that identifies any taxonomic group to be edge sensitive in that they differentially utilized edge or core areas of seagrass patches. The one exception may be infaunal bivalves which appear to act as "interior" species in the majority of studies surveyed here. This group then would be expected to exhibit a disproportionate decrease in abundance as patch size decreases, as may occur with fragmentation of the habitat.

The data for fish and amphipods from *Halodule* beds in Tampa Bay did not reveal strong evidence for total fish or amphipod density to be related to seagrass patch size. This was also true for dominant fish and amphipod species. Moreover small patches did not appear to be of poor quality for either fish or amphipods given that densities in both smallest and largest beds were often similar and no species were found to be missing from small versus large patches (Bell, unpublished). These findings depart from those of McNeill and Fairweather (1993) who found increased densities of selected fish species in the eight smallest beds of *Posidonia* seagrass.

Factors other than patch size might impact faunal densities in seagrasses. Terrestrial studies have suggested that degree of isolation and position of patches in landscapes might explain a lack of a patch size effect (Burke and Goulet, 1998). In a review comparing the relative contribution of various patch characteristics as

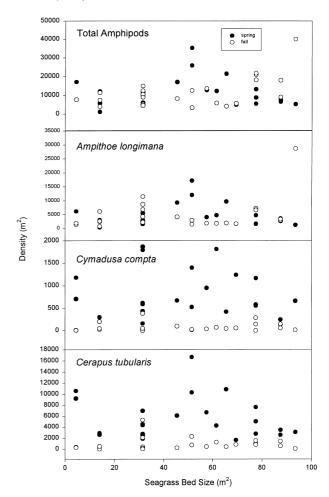


Fig. 2. Seasonal densities for total amphipods and three most dominant amphipod species within *Halodule wrightii* beds of various sizes, spring and fall 1994–1995.

predictors of faunal abundance or species richness, Mazerolle and Villard (1999) concluded that landscape characteristics were significant predictors of abundance for a wide variety of terrestrial species. In the marine habitat, Bell et al. (1995) showed experimentally that patches of similar dimension and age captured different amounts of macroalgae (which has no behavior) when placed at different sites, suggesting that delivery and/or interception of organisms is of major importance in this system. Clearly, in addition to individual patch characteristics which have received attention in past studies (Table 1), the landscape context will need to be considered in marine systems (Robbins and Bell, 1994; Micheli and Peterson, 1999) and may provide an explanation for the enigmatic increase in faunal abundance of fish and amphipods in particular seagrass beds in Tampa Bay which are neither consistently the largest nor smallest in dimension.

The edge effects uncovered for polychaetes appear to be linked to factors that operate over a small spatial scale (m). Results for *Kingbergonuphis simoni* confirmed that spatial distribution of this infaunal polychaete's

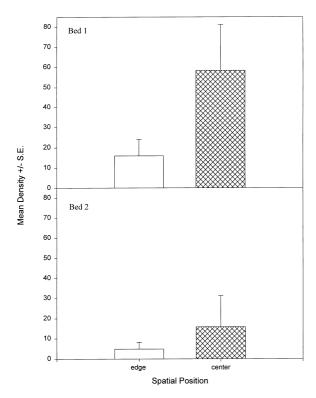
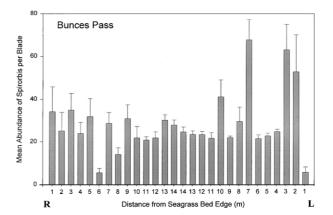


Fig. 3. The density of *Kingbergonuphis simoni* in the edge and interior of *Halodule wrightii* beds from Lassing Park, in June 1990.

abundance differed between center and edges of beds, with significantly lower densities consistently recovered from edge areas of *Halodule* beds. The two beds surveyed in this study were of similar size and age, had no significant difference in seagrass densities (Bell et al., 1993), and were located within 20 m of each other. Thus, the overall densities were probably influenced by some very localized impacts. Higher reproductive success of this brooding polychaete in bed 1 may explain the differences in densities but data were not available to evaluate this idea. Determining the underlying mechanisms for such "interior" aggregations of *K. simoni* awaits detailed studies on resource utilization and reproduction of this species in the different regions of a seagrass bed.

Density of *Spirorbis spirillum* epiphytic on seagrass blades collected from *Thalassia* seagrass beds was reduced at edges compared to more interior locations of the bed. However, edge effects were only present at one end of the sampling transect (e.g. along only one edge). Some of the edge effects exhibited by *S. spirillum*, as well as those detected in earlier studies for some taxa, may be linked to the modification of water flow by vegetation structure (Fonseca et al., 1982) and thus food supply and larval recruitment. Patterns in growth of other seagrass species have also been shown to have strong edge effects or changes in densities proceeding from edge to center of beds (Irlandi, 1997) and in some cases, distinct morphologies along the flood edge (Fonseca, 1998; Jensen and Bell, 2001). Hydrodynamic factors may influence



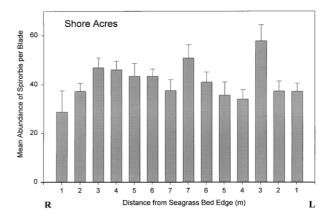


Fig. 4. The mean (+/- S.D.) of number of *Spirorbis spirillum* \times blade⁻¹ on *Thalassia testudinum* seagrass blades along a transect across a bed at Bunces Pass and Shore Acres, October 1994. R and L refer to terminal ends of the transect spanning the bed.

such patterns of seagrass growth (Jensen, 1998) and thus play a role in producing the patterns reported for *S. spirillum*, which has a short-lived larval form. Understanding the role of edges may be the key to deciphering how faunal community dynamics change as habitat complexity is altered (Fagan et al., 1999) but our survey and results which show faunal response at edges to be highly site and taxon specific, do not portend that simple descriptions of community change related to seagrass fragmentation will be forthcoming.

While our studies in Tampa Bay focused upon measures of faunal density to discern edge or patch size effects, other studies have measured growth or predation at edges of seagrass patches (Irlandi, 1997; Bologna and Heck, 1999; Irlandi et al., 1999). Bologna and Heck (1999) reported higher densities of scallops at edges of seagrass beds but were unable to explain how organismal growth and/or differential risk of predation could account for this pattern. Irlandi (1997) found an increased growth rate of clams introduced into the center of large versus small beds, but no natural increased abundance of organisms was recorded there. These studies further illustrate that advancing our understanding of the effects of fragmentation on seagrass associated fauna

will benefit from both assessment of spatial distributions and evaluation of demographic and/or behavioral features of fauna. Monkkonen and Reunanen (1999) argue that the current knowledge of critical habitat characteristics of most species is not sufficient to make precise predictions as to what level of fragmentation results in a decrease of the viability of faunal populations; this appears to apply amply to the seagrass ecosystem.

Several distinctions emerge from studies on fauna and fragmentation or habitat loss in marine settings, especially in comparison to their terrestrial counterparts. First, many of the experimental seagrass studies utilized patches that were relatively small in dimension. For example, Eggleston et al. (1998) used patches that ranged in size from 0.25 to 2 m². Few studies on the natural grassbeds have included surveys or experiments in "large" patches that exceed 10 m in diameter (e.g. Irlandi, 1996, 1997). Comparatively, terrestrial studies on fragmentation often focus on patches extending over 100s to 1000s of hectares (e.g. McCoy and Mushinsky, 1994). Impacts of patch size may only be detected in large patches where different core and edge microhabitats can be established and this may vary in different hydrodynamic regimes. Results from our epibenthic polychaete study showed that only in the larger bed was an edge effect detected. Moreover, in some marine systems the patches of seagrasses themselves may be temporally dynamic, displaying marked dimensional changes within season or year linked to hydrodynamic conditions (Bell et al., 1999; Turner et al., 1999). Thus any fauna-patch size effect may be temporally variable and difficult to detect (e.g. Hovel, 1999). Finally, it is difficult to test experimentally the effects of fragmentation on marine fauna over large spatial scales as underwater landscapes are not readily manipulated nor do typically adequate maps of submerged habitat over temporal scales that are necessary to examine this topic exist (Robbins, 1998b).

In many of the faunal studies in seagrass patches, impacts of fragmentation and habitat loss may be difficult to detect because spacing between remnant patches may be insufficient to hinder dispersal, given the role of passive movement with water currents that distribute organisms among patches (Robbins and Bell, 1994). We are unaware of any studies that examine the question of faunal dispersal across a habitat undergoing fragmentation within a marine system (cf. With et al., 1999). Conceivably, some of the impacts of fragmentation on fauna in seagrass systems may only be observed when a greater degree of isolation among seagrass patches exists than that typically included in past studies. Results from Collinge (1998) on grassland insects support this suggestion to some degree in that she found that the presence of large-sized species was not reduced in fragmented habitats because the interpatch distance was small among the patches; organisms in this case

may have been using the habitat as one large patch. However, the influence of corridors may be reduced in marine systems as both active and passive dispersal of organisms in the water column allow for facilitated transport over large spatial scales. Moreover, some seagrass systems exist naturally as discontinuous patches within a sand matrix because of the hydrodynamic setting (Fonseca and Bell, 1998) so that fragmentation events may not produce spatial distributions of patches that are uncommonly encountered by fauna.

Under what scenario might we expect loss of seagrass habitat or fragmentation to translate into some measurable response by fauna? Given that many marine organisms can move among patches, the spatial scale over which to detect differences may need to be larger than that previously investigated. Events such as extensive seagrass die off or a high incidence of boat propellerdamage over an extremely large area may be required to detect effects of habitat fragmentation on faunal abundances. Large scale seagrass modification by intense propeller scarring may lead to the most dramatic changes in seagrass beds and faunal associates because scarring may not only remove seagrass but also cause the landscape to lose integrity as margins erode after fragmentation (Fonseca and Bell, 1998). As seagrass fragmentation increases, the area over which sediment binding by seagrass vegetation occurs should likewise decrease, with sediments becoming more easily suspended; this may be most severe along edges where currents are greatest (Walker, 1989). Here the impacts of fragmentation by human activities such as anchor moorings and prop scarring may have major implications on bed persistence by changing the morphology of seagrass patches. If the latter is true, then there may be some threshold of plant removal beyond which the impacts on seagrass ecosystems, including faunal composition and abundance, might be severe (e.g. the 59% level sensu Fonseca and Bell, 1998). Likely candidates to meet these criteria are sites such as the Florida Keys where boating activities are very common in shallow areas (M.O. Hall, personal observation). Thus, plans for seagrass conservation should include an assessment of the threshold limits for maintaining seagrass bed integrity and we expect that these limits will vary with seagrass species and the hydrodynamic setting (Fonseca and Bell, 1998).

Finally, our findings for faunal and seagrass patch size provide information for designing seagrass restoration programs. Fonseca and Bell (1998) discussed how seagrass patch sizes differ with physical setting showing how high exposure sites typically had discontinuous seagrass beds whereas low exposure sites typically had more continuous seagrass cover. In recommendations for designing seagrass restoration sites, Fonseca et al. (1998) advocated construction of patches of sizes similar to that which is characteristic of the site. Of concern, however, is that seagrass patches support sufficient

densities of fauna, such that they can be considered functionally equivalent to that of natural beds. Our findings here, and those from a variety of studies, suggest that seagrass patch size by itself does not appear to adequately account for variation in faunal abundance (see also Turner et al., 1999) and may not be a critical feature for restoration design. Therefore sites where natural seagrass patches are represented by continuous seagrass cover, may need not necessarily construct large replanted patches in order to support a functionally equivalent fauna — equivalent area of smaller patches may be sufficient. Instead, efforts to identify areas with similarity of landscape context or patch characteristics other than patch size may be more crucial to maintain similar faunal assemblages in restored areas (Bell et al., 1997). This suggestion has received support in some terrestrial studies where restoration "site" selection influenced successful establishment of target fauna (e.g. Robinson and Handel, 1991; McChesney et al., 1995) and from marine studies of fauna in mixed habitats (Irlandi and Crawford, 1997; Micheli and Peterson, 1999). Additional studies on fauna and seagrass landscape features will now be required to identify and evaluate seagrass landscape metrics other than patch size that might be critical to establishment and maintenance of seagrass faunal assemblages.

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References

- Allison, G.W., Lubchenco, J., Carr, M.H., 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications 8, 579–592.
- Bell, S.S., Clements, L.A.J., Kurdziel, J.P., 1993. Macrobenthic production in natural and restored seagrass beds: a case study of the polychaete, *Kingbergonuphis simoni*. Ecological Applications 3, 610–621.
- Bell, S.S., Hall, M.O., Robbins, B.D., 1995. Toward a landscape approach in seagrass beds: using macroalgal accumulation to address questions of scale. Oecologia (Berl.) 104, 163–168.
- Bell, S.S., Fonseca, M.S., Motten, L.B., 1997. Linking restoration and landscape ecology. Restoration Ecology 5, 318–323.
- Bell, S.S., Robbins, B.D., Jensen, S.L., 1999. Gap dynamics in a seagrass landscape. Ecosystems 2, 493–504.
- Bender, D.J., Contresas, T.A., Fahrig, L., 1998. Habitat loss and population decline: a meta analysis of the patch size effect. Ecology 79, 517–533.
- Bologna, P.X., Heck Jr., K., 1999. Differential predation and growth rates of bay scallops within a seagrass bed. Journal of Experimental Marine Biology and Ecology 239, 299–314.
- Burke, D., Goulet, H., 1998. Landscape and area effects on beetle assemblages in Ontario. Ecography 21, 472–479.
- Collinge, S.K., 1998. Spatial arrangement of habitat patches and corridors: clues from ecological field experiments. Landscape Urban Planning 42, 157–162.

- Dirnberger, J.M., 1990. Benthic determinants of settlement for planktonic larvae: availability of settlement sites for the tube building polychaete *Spirorbis spirillum* (Linneaus) settling onto seagrass blades. Journal of Experimental Marine Biology and Ecology. 140, 89–105.
- Eggleston, D.B., Etherington, L.L., Ellis, W.E., 1998. Organism response to habitat patchiness: species and habitat dependent recruitment of decapod crustaceans. Journal of Experimental Marine Biology and Ecology 223, 111–132.
- Eggleston, D.B., Ellis, W.B., Etherington, L.L., Dalhgren, C.P., Posey, M.H., 1999. Organism responses to habitat fragmentation and diversity: habitat colonization by estuarine macrofauna. Journal of Experimental Marine Biology and Ecology 236, 107–132.
- Fagan, W.F., Cantrell, R.S., Cosher, C., 1999. How habitat edges change species interactions. American. Naturalist 153, 165–182.
- Fonseca, M.S., 1998. Exploring the basis of pattern expression in seagrass landscapes. PhD dissertation, University of California, Berkeley.
- Fonseca, M.S., Kenworthy, W.J., Courtney, F.X., 1996. Development of planted seagrass beds in Tampa Bay, Florida, USA. I. Plant components. Marine Ecology Progress Series 132, 127–139.
- Fonseca, M.S., Bell, S.S., 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Marine Ecology Progress Series 171, 109–121.
- Fonseca, M.S., Fisher, J.S., Zieman, J.C., Thayer, G.W., 1982. Influence of the seagrass *Zostera marina* L. on current flow. Estuarine and Coastal Shelf Science 15, 351–364.
- Fonseca, M.S., Kenworthy, W.J., Thayer, G.W., 1998. Guidelines for the Conservation and Restoration of Seagrasses in the United States and Adjacent Waters (NOAA Coastal Ocean Program Decision, Analysis Series #12). NOAA Coastal Ocean Office, Silver Spring MD
- Forman, R.T.T., 1995. Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, UK.
- Frost, M.T., Rowden, A.A., Altril, M.J., 1999. Effect of habitat fragmentation on macroinvertebrate infaunal communities associated with the seagrass *Zostera marina* L. Aquatic Conservation: Marine and Freshwater Ecosystems 9, 255–263.
- Hastings, K., Hesp, P., Kendrick, G.A., 1995. Seagrass loss associated with boat moorings at Rottnest Island, Western Australia. Ocean & Coastal Management 26, 225–246.
- Herkert, J.R., 1994. The effects of habitat fragmentation on midwestern grassland bird communities. Ecological Applications 4, 461–471.
- Hovel, K.A., 1999. The effects of seagrass habitat fragmentation on juvenile blue crab survival. PhD thesis, College of William and Mary
- Irlandi, E.A., 1994. Large and small scale effects of habitat structure on rates of predation: how percent cover of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. Oecologia (Berl.) 98, 176–183.
- Irlandi, E.A., 1996. The effects of seagrass patch size and energy regime on growth of a suspension feeding bivalve. Journal of Marine Research 54, 161–185.
- Irlandi, E.A., 1997. Seagrass patch size and survivorship of an infaunal bivalve. Oikos 78, 511–518.
- Irlandi, E.A., Ambrose Jr, W.G., Orlando, B.A., 1995. Landscape ecology and the marine environment: how spatial configuration of seagrass habitat influences growth and survival of the bay scallop. Oikos 72, 307–313.
- Irlandi, E.A., Crawford, M.K., 1997. Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. Oecologia 110, 222–230.
- Irlandi, E.A., Orlando, B.A., Ambrose, W.A., 1999. Influence of seagrass habitat patch size on growth and survivorship of the juvenile bay scallop, *Argopecten irradius concentricus* (Say). Journal of Experimental Marine Biology and Ecology 235, 21–43.

- Jensen, S.L., 1998. Below ground morphological plasticity of the seagrass, *Halodule wrightii* in relation to sediment resources. PhD dissertation, University of South Florida, Tampa, FL.
- Jensen, S.L., Bell, S.S., 2001. Seagrass growth and patch dynamics: cross scale morphological plasticity. Plant Ecology (in press).
- McNeill, S.E., Fairweather, P.G., 1993. Single large or several small marine reserves? An experimental approach with seagrass fauna. Journal of Biogeography 20, 428–440.
- Mazerolle, M.J., Villard, M.A., 1999. Patch characteristics and landscape context as predictors of species presence and abundance: A review. Ecoscience 6, 117–124.
- McChesney, C.J., Koch, J.M., Bell, D.T., 1995. Jarrah forest restoration in western Australia: canopy and topographic effects. Restoration Ecology 3, 105–110.
- McCoy, E.D., Mushinsky, H.R., 1994. Effects of fragmentation on richness of vertebrates in the Florida scrub. Ecology 75, 446–457.
- Micheli, F., Peterson, C.H., 1999. Estuarine vegetated habitats as corridors for predator movements. Conservation Biology 13, 869– 877.
- Monkkonen, M., Reunanen, P., 1999. On critical thresholds in landscape connectivity: a management perspective. Oikos 84, 302–305
- Pulich, W.M., White, M.A., 1991. Decline of submerged vegetation in the Galveston Bay system. Chronology and relationships to physical processes. Journal of Coastal Research 7, 1125–1138.
- Robbins, B.D., 1998a. The dynamics of a changing landscape: an example using a subtidal seagrass dominated landscape. PhD thesis, University of South Florida, Tampa, FL, USA.
- Robbins, B.D., 1998b. Quantifying temporal change in seagrass areal cover: the use of GIS and low resolution aerial photography. Aquatic Botany 58, 259–267.
- Robbins, B.D., Bell, S.S., 1994. Seagrass landscapes: a terrestrial approach to the marine subtidal environment. Trends in Ecology and Evolution 9, 301–304.
- Robbins, B.D., Bell, S.S., 2000. Landscape dynamics: an example using a subtidal seagrass dominated landscape. Ecology 81, 1193– 1205.
- Robinson, G.R., Handel, S.N., 1991. Forest restoration on a closed landfill: rapid addition of new species by bird dispersal. Conservation Biology 7, 271–278.

- Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M.L., Fitch, M.S., Martinko, E.A., 1992. Diverse and contrasting effects of habitat fragmentation. Science 257, 524–526.
- Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation. A review. Conservation Biology 5, 18–32.
- Short, F.T., Willy-Echeverria, S., 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation 23, 17–27.
- Thayer, G.W., Kenworthy, W.J., Fonseca, M.S., 1984. The ecology of seagrass meadows of the Atlantic coast: a community profile. US Fish and Wildlife service. FWS/OB5-84/02.
- Turner, S.J., Hewitt, J.E., Wilkinson, M.R., Morries, D.J., Thrush, S.F., Cummings, V.J., Funnell, G., 1999. Seagrass patches and landscapes: the influence of wind wave dynamics and hierarchical arrangement of spatial structure on macrofaunal seagrass communities. Estuaries 22, 1016–1032.
- Trzcinski, M.K., Fahrig, L., Merriam, G., 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications 9, 586–593.
- Villard, M.A., Trzcinski, M.K., Merriam, G., 1999. Fragmenation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conservation Biology 13, 774–784.
- Virnstein, R.R., Howard, R.K., 1987. Motile epifauna of marine macrophytes in the Indian River lagoon, FL. Comparisons among three species of seagrasses from adjacent beds. Bulletin of Marine Science 41, 1–12.
- Vos, C.C., Stumpel, A.H.P., 1995. Comparison of habitat isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla arborea*). Landscape Ecology 11, 203–214.
- Walker, D.I., Lukatelich, R.J., Bastyan, G., McComb, A.J., 1989.Effect of boat moorings on seagrass beds near Perth Western Australia. Aquatic Botany 36, 69–77.
- Wilcox, B., Murphy, D., 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist 125, 879–887.
- Wilson, D.P., 1949. The decline of *Zostera marina* L. at Salcombe and its effects on the shore. Journal of the Marine Biological Association of the United Kingdom 28, 395–412.
- With, K.A., Cadaret, S.J., Davis, C., 1999. Movement responses to patch structure in experimental fractal landscapes. Ecology 80, 1340–1353.